

CONSERVATION STATUS OF *CAREX ORONENSIS*
(CYPERACEAE), A MAINE ENDEMIC

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ABSTRACT. *Carex oronensis*, Orono sedge, is Maine's only known endemic plant species. From 1916 through 1986 only one individual was collected. From 1986–1998, we and others found 58 populations and approximately 2862 reproductive individuals in early successional habitats, almost exclusively in the Penobscot River drainage. Of extant populations, 80% have < 20 plants, and 22% have only 1–2. In a Principal Coordinates Analysis with 22 morphological variables and 95 individuals, *C. oronensis* separated completely from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria*. Canonical Discriminant Analysis resulted in 100% classification for 19 individuals of *C. oronensis*. *Carex oronensis* differs from the four other taxa especially in perigynium features: narrow wings, lack of abaxial nerves, glossy texture, rust-colored blotch (68% of sample), and lack of basal sponginess about the achene. Species status is appropriate for *C. oronensis* because it is fertile, its offspring are identical to the parent, and it is morphologically distinct. Because its distribution is wholly north of the Wisconsin glacial boundary and it is not clearly adapted for long-distance dispersal, the species appears to have arisen in Maine. Hay transport by the lumber industry could account for the spread of *C. oronensis* within the Penobscot River drainage and its confinement there. Mowing after seed dispersal in mid-July appears to benefit populations.

Key Words: *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, *C. tinctoria*, *Carex* section *Ovales*, Cyperaceae, Orono sedge, morphology, Maine, plant endemism, plant conservation

Conservation of species is often prioritized according to endemism, and plant endemism is unusual in northeastern North America (Gentry 1986). *Carex oronensis* Fernald is apparently the only plant species endemic to Maine (Dibble et al. 1989). Two other *Carex* species, *C. elachycarpa* Fernald and *C. josselynii* (Fernald) Mack. ex Pease, were considered narrow endemics (Fernald 1950) until Reznicek and Ball (1979) placed them in synonymy with *C. sterilis* Willd. and *C. echinata* Murray, re-

spectively. Until February 28, 1996, *C. oronensis* was listed in the Federal Register of Endangered and Threatened Plant Species as Category 2, a designation for taxa requiring taxonomic resolution and/or further information about distribution. On that date, Category 2 was eliminated by the U.S. Fish and Wildlife Service because of uneven data quality and insufficient resources to track the more than 3000 species in this category (Office of the Federal Register 1996). *Carex oronensis* was listed as state Endangered due to restricted global distribution (Dibble et al. 1989), but is currently listed as state Threatened because > 50 populations have been documented. It is proposed for state Special Concern due to apparent lack of immediate threats. It is currently considered "S2" and "G2" using the Natural Heritage ranking system (Haines and Vining 1998).

Carex oronensis is a member of section *Ovales* Kunth, the largest section in the genus, in which identification is "notoriously difficult" (Reznicek and Catling 1986) because the numerous species are morphologically similar, gaps between some species are narrow (though deep; A. A. Reznicek, pers. comm.), and for some species groups there has not yet been sufficient taxonomic study to resolve questionable species. Some species apparently intergrade (Whitkus 1988) or hybridize with other species (Fernald 1950; Gleason and Cronquist 1991). The section occurs mostly in temperate North America, with some species in montane regions of Central and South America. Two Eurasian members of section *Ovales*, *C. macloviana* d'Urv. and *C. ovalis* Gooden. (= *C. leporina* L.), are found in North America. The former is unique among *Ovales* in its bipolar distribution (Moore and Chater 1971) and is more or less frequent in Alaska and northwest Canada but is otherwise rarely found in the conterminous United States. *Carex ovalis* is thought to be introduced. In Maine, sect. *Ovales* is represented by 22 species and one variety, more taxa than any other section of the genus (Campbell et al. 1995).

Fernald (1902) named *Carex oronensis* after Orono, the type locale and the town in which he began his botanical activities. Most authors recognize *C. oronensis* at the species level (Fernald 1950; Kartesz 1994). On the other hand, Gleason and Cronquist (1991) suggested that it is a hybrid but specified no putative parents. Early collections of *C. oronensis* were from the southern Penobscot River drainage (Eastman 1980; Figure 1) and date from 1889–1916. Between 1916 and 1986, only one individual

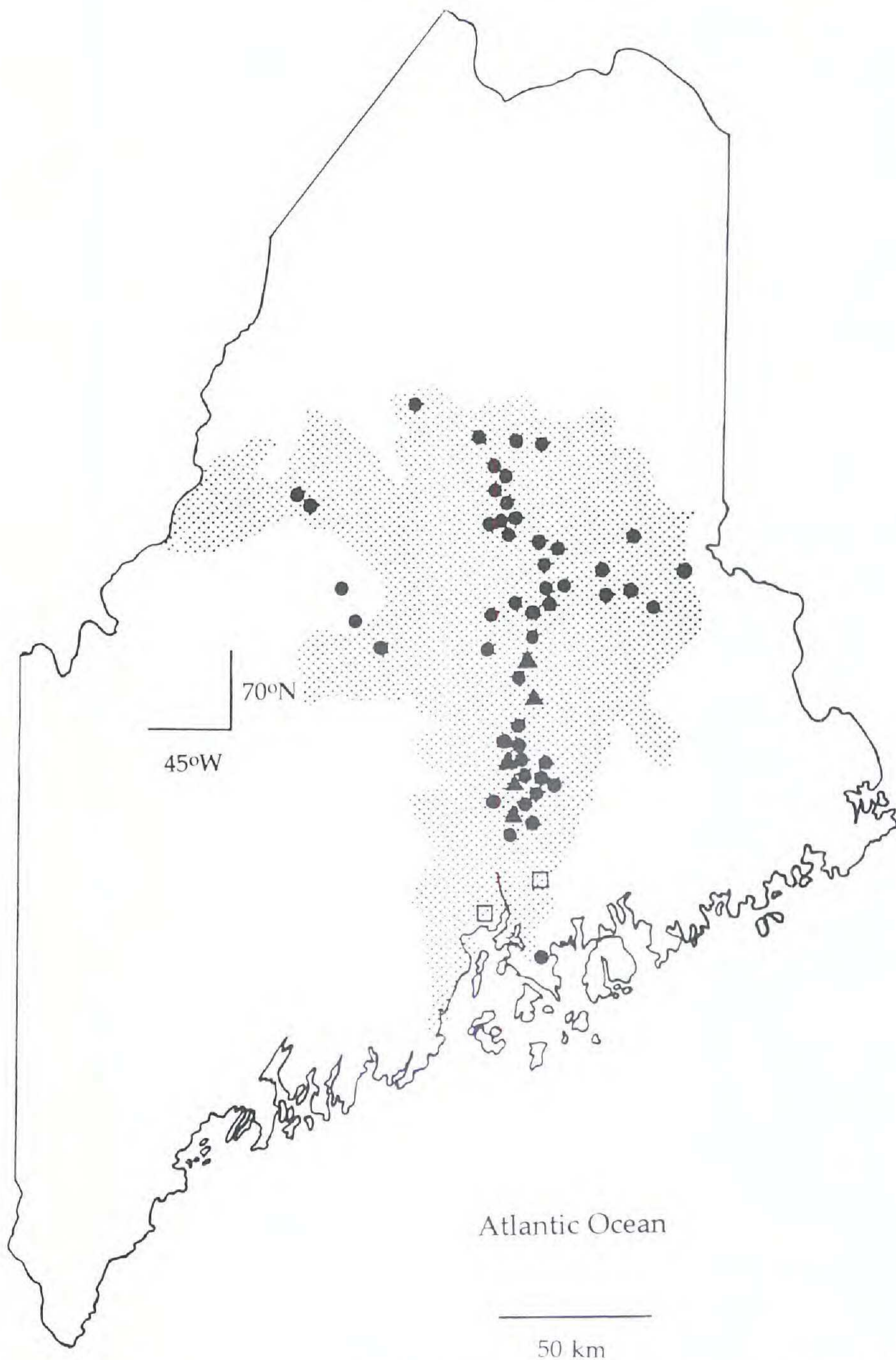


Figure 1. Distribution of occurrences of *Carex oronensis*, all in Maine, U.S.A. showing two unlocated pre-1916 (empty squares) and 53 post-1916 (filled circles) sites. Three of the filled circles represent multiple sites in Orono—where density is highest. Current sites in five townships (filled triangles) could be re-located historic sites, although exact locales for historic collections are unknown. The shaded area is the approximate extent of the Penobscot River drainage.

was collected. Until this study (Dibble 1991), little was known of the morphological distinctness, population size, current distribution, ecology, or reproductive biology for this species.

Our primary objective was to ascertain conservation status of *Carex oronensis*. We sought to determine its geographic distribution, test its morphological distinctness, obtain a chromosome number, characterize its breeding system, describe its habitat, and see with which other members of *Carex* in sect. *Ovales* it grows.

MATERIALS AND METHODS

We conducted field surveys for *Carex oronensis* intensively from 1987–89 and intermittently from 1990–98 within about 80 km of the Penobscot River valley (Figure 1). At each site we collected at least one mature specimen of *C. oronensis* (vouchers at MAINE) and all sympatric members of sect. *Ovales*, and we counted plants of *C. oronensis*, listed associated vegetation, and recorded habitat type. We counted a discrete clump of stems as a *C. oronensis* individual and included only fruiting plants because we cannot identify some members of sect. *Ovales* without mature perigynia.

In a preliminary survey of herbarium material, we examined approximately 600 herbarium specimens, including representatives of all North American and Eurasian species in sect. *Ovales* known to us except *Carex maackii* Maxim. and *C. planata* Franch. & Sav. of Eurasia (Fernald 1950; Gleason and Cronquist 1991; Hermann 1974; Kartesz 1994; Mackenzie 1931–1935) from 14 herbaria (BH, CR, MAINE, MICH, MT, NEBC, NHA, NY, NYS, TRT, UNB, US, VT, and WELC; abbreviations in Holmgren et al. 1990). We also examined approximately 290 specimens we obtained in Maine, New Brunswick, Newfoundland, and Costa Rica. Many of the new collections from Maine and New Brunswick were determined or annotated by P. E. Rothrock and A. A. Reznicek.

Initially we included 12 species in sect. *Ovales* that overlap with *Carex oronensis* in geographic range and that resemble this species in morphology, habit, and habitat requirements. We selected for numerical analysis in the morphological study, those specimens within each taxon that represent the full range of apparent morphological variation. We evaluated 54 characters compiled from taxonomic treatments and from herbarium and field observations, then eliminated 32 characters from the preliminary

data set because of high variability within and considerable overlap among taxa.

The preliminary analysis identified three species—*Carex ovalis*, *C. tinctoria* Fernald, and *C. bebbii* Olney—and one variety, *C. scoparia* Schkuhr ex Willd. var. *tessellata* Fernald & Wiegand, as morphologically closest to *C. oronensis*. *Carex scoparia* var. *tessellata* has been found in Maine only locally along the coast east of Penobscot Bay. We used only these five taxa in further analysis, with 19 specimens per taxon (Appendix). For *C. ovalis*, we used nine specimens from North America (but not from Maine, where it is rare), nine specimens from Eurasia, and one from New Zealand. Some character states shared by these five taxa (including *C. oronensis*) are loosely cespitose habit (versus densely cespitose or rhizomatous), (3) 4–8 (9) spikes per inflorescence, spike arrangement aggregate (versus moniliform), pistillate scales dark reddish brown with a lighter midvein, and perigynia usually less than 2.5 mm wide. Vegetative characters of *Carex* useful in other studies or floras (Damman 1963; Haines and Vining 1998; Reznicek and Catling 1986; Rothrock 1991; Standley 1989) proved to be of little value in separating *C. oronensis* from the four other taxa in this study. As we could find no vegetative characters that reliably separate these taxa from one another, we included only characters that relate to the inflorescence and associated structures. Limitation of taxonomically useful characters to those associated with the inflorescence in this study parallels work in *Carex* sect. *Montanae* (Crins and Ball 1983). Our study was directed toward distinguishing *C. oronensis* and we did not explore variables that could separate *C. ovalis* and *C. tinctoria* more definitively. We visually assessed characters using box plots (McGill et al. 1978) in SYSTAT (Version 6.0; SPSS, Evanston, IL). Differences between groups were determined by lack of overlap between the notched portion of boxes on a horizontal axis, and from means and standard deviations.

We scored 10 continuous, 1 discontinuous, and 11 attribute characters (Table 1) for 19 specimens each (total 95) in *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria* (Appendix). The number of populations sampled for each taxon ranged from 10–19. For all characters and most specimens, we used the mean of five replicate measurements per individual (i.e., five different perigynia from one specimen) to account for

Table 1. Twenty-two morphological characters and their states used in the Principal Coordinates Analysis of *Carex oronensis* and four Maine taxa that resemble it. The ten continuous characters (noted as *) were also used in a Canonical Discriminant Analysis. All measurements in mm. "0" indicates absence, "1" presence.

Structure	Character	Character States or Units
Inflorescence	Extent of aggregation	0 – open, the spikelets separate, 1 – tightly aggregate
Pistillate scales	Color	0 – not chestnut-brown, 1 – chestnut-brown
	Length*	mm
Perigynium	Width*	mm
	Length*	mm
	Width*	mm
	Distance from base to widest part*	mm
	Distance from base to first serrulation*	mm
	Beak color	0 – light, 1 – dark
	Beak margin	0 – dark, 1 – hyaline
	Base	0 – without stipe, 1 – substipitate
Adaxial surface	0 – without blotch, 1 – rust-colored blotch	

intraplant variation; single measurements accounted for < 5% of the overall dataset.

For the 95 individuals, we conducted a Principal Coordinates Analysis (PCOR), which is recommended for mixed continuous, discontinuous, and attribute characters, in the NTSYS-PC software (Version 1.8; Exeter Publishing Ltd., 100 North Country Rd., Bldg. B, Setauket, NY 11733), and calculated Gower's similarity coefficient using the GOWER3 program (T. A. Dickinson, Vascular Plant Herbarium, Royal Ontario Museum, Toronto, ON, Canada). To see how well groups separate on the basis of the 10 continuous characters (Table 1), and to find the most discriminating of these characters, we conducted Canonical Discriminant Analysis (CDA) with stepwise variable selection in SYSTAT. We examined the continuous characters in an ANOVA and post hoc multiple comparisons using Tukey's Studentized Range (HSD) test ($\alpha = 0.05$) with Bonferoni adjustments.

To determine chromosome number, we fixed inflorescence buds of *Carex oronensis* in the early morning in Farmer's Solution

Table 1. Continued.

Structure	Character	Character States or Units
	Texture of adaxial surface	0 – dull, 1 – pearly
	Wing tooth color	0 – light, 1 – dark
	Adaxial surface	0 – nerves weak, 1 – nerves prominent
	Abaxial suture margin	0 – light, 1 – hyaline adaxial
	Nerves	Count
	Base of achene	0 – not surrounded by spongy tissue, 1 – spongy
	Wing width*	mm
Achene	Length*	mm
	Width*	mm
	Stipe length*	mm

(3:1 absolute alcohol:acetic acid, by volume) for 24 hr. and stored them at 5°C in 70% ethanol. We squashed anthers and stained with acetocarmine. Chromosome counts were obtained from cells in late prophase I using a Zeiss Standard microscope.

We tested for self- and cross-compatibility using seven individuals of *Carex oronensis* and two each of *C. tinctoria* and *C. tenera* Dewey, which we dug from natural populations, mostly in Orono, and maintained as potted individuals in a greenhouse. To determine if these species were self-compatible, we bagged intact inflorescences prior to anther dehiscence on three individuals of *C. oronensis* and one each of *C. tinctoria* and *C. tenera*. Seeds from open pollinations of *C. oronensis* were planted in a common garden to determine whether the species would breed true.

To test pollen viability in five *Carex oronensis* individuals, we immersed fresh pollen from five anthers per plant in two drops of Alexander's (1969) pollen stain on a glass slide and examined after 2 min. at $\times 1600$. We counted more than 200 grains for each sample. Red-staining pollen grains were counted as unaborting, and those that stained green were considered aborting. As stainability does not necessarily indicate germinability, we also germinated fresh pollen from five anthers each for four individuals of *C. oronensis* on glass slides in two drops of germination medium (agar, 2.5 g; H₂O, 250 ml; sucrose, 107 g; CaNO₃, 0.07 g; Boron, 0.07 g; adapted from Stanley and Linskens 1974) for 24 hr. at room temperature and then examined for germinability at

×1600. We scored more than 200 pollen grains per sample for pollen tube growth.

We germinated open-pollinated seeds from five individuals of *Carex oronensis* in the light on moist filter paper following six weeks of cold storage at 5°C. We used frequency of filled achenes as an estimate of fruit set in five individuals of *C. oronensis* selected from different parts of the species range, with a sample of 28 flowers per individual.

RESULTS

Morphological study. We determined that no species in *Carex* section *Ovales* from Mesoamerica or from western or southeastern North America was as close morphologically to *C. oronensis* as species from northeastern North America and Eurasia. We found *C. oronensis* to be a distinct entity and we present a description based on our measurements (see below). In an ordination plot of the first and second Principal Coordinates based on 22 variables, *C. oronensis* and *C. bebbii* each separated well from *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tincta* (Figure 2). The failure of these latter three taxa to form distinct clouds was not because they were difficult to distinguish from each other but because we emphasized characters that differentiated *C. oronensis*. Higher dimensions failed to resolve *C. oronensis* and were otherwise relatively uninformative. The first two Principal Coordinates accounted for 31.5 and 26.6%, respectively, of the total variation in the original variable space, or a total of 58.1%. *Carex oronensis* is closest to *C. ovalis* and *C. tincta*. These latter two did not separate on the basis of the characters examined.

Canonical Discriminant Analysis on seven continuous characters selected by stepwise analysis resulted in perfect classification of *Carex oronensis* and *C. bebbii* (Table 2). The other three taxa classified at least 80% correctly, with three individuals of *C. ovalis* classifying as *C. tincta*. Plots of various combinations of the first three canonical axes failed to show a discrete cloud for any taxon but *C. oronensis* (not shown).

Carex oronensis differed markedly from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tincta* (Figure 3) in perigynium width, perigynium wing width, and achene stipe length (Table 3; Figures 4d, 4h, 4l). The number of perigynium abaxial nerves was higher in *C. oronensis* than in the other taxa (Figure 4g).

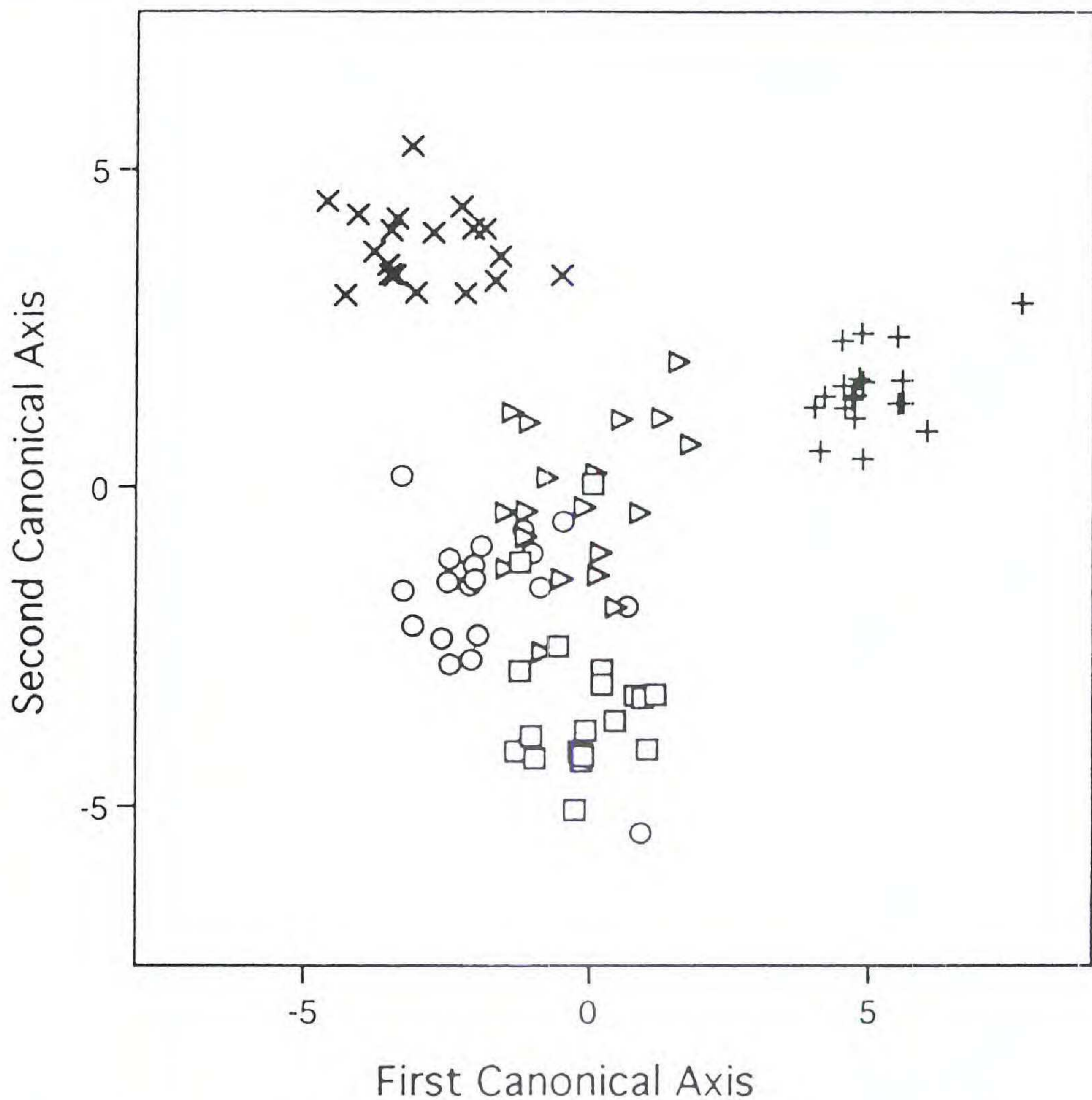


Figure 2. Plot of Principal Coordinates Analysis for 22 morphological characters and 19 specimens each of *Carex bebbii* (+), *C. oronensis* (X), *C. ovalis* (circle), *C. scoparia* var. *tessellata* (square), and *C. tincta* (triangle).

Carex oronensis differed from at least one other taxon in 11 of the 12 quantitative variables (Figures 4a–4l, but not 4i). *Carex oronensis* and *C. tincta* differed from the other three taxa in perigynium scale length (Figure 4a). *Carex oronensis*, *C. tincta*, and *C. ovalis* were distinguished from *C. bebbii* and *C. scoparia* var. *tessellata* in perigynium scale width (Figure 4b), perigynium length (Figure 4c), and distance from the base of the perigynium to the first serrulation (Figure 4f). Achene width was similar in *C. oronensis*, *C. bebbii*, and *C. scoparia* var. *tessellata* (Figure 4k).

In addition to the narrow perigynium and short achene stipe of *Carex oronensis* (Table 3), qualitative characters we found useful

Table 2. Canonical loadings, discriminant function (a), and table of frequencies (b) for classifying *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria* based on seven morphological characters.

a) Canonical loadings and discriminant function.

Character	Canonical Loadings		Discriminant Function				
	1	2	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tinctoria</i>
Constant			-106.07	-185.70	-213.39	-198.82	-175.76
Pistillate scale length	-0.84	0.18	22.93	34.74	39.86	34.64	25.10
Pistillate scale width	-0.51	-0.38	68.11	105.06	94.62	83.24	93.59
Perigynium length	-0.61	0.44	35.33	44.69	42.75	52.96	43.74
Distance from base of perigynium to wing serrulation	-0.36	-0.34	-3.37	-1.54	0.16	-15.19	1.63
Distance from base to widest part of perigynium	-0.30	0.18	-5.35	-9.46	-10.67	-6.50	-9.65
Perigynium wing width	0.24	0.57	-21.39	-82.93	-313.84	-28.10	-27.41
Achene width	0.14	0.07	-10.38	-30.06	-11.04	-21.06	-5.21

Table 2. Continued.

b) Frequencies, showing observed (rows) and predicted (columns) number of individuals classified, with percent in parentheses. Correct classifications in bold.

Taxon	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>	Total
<i>bebbii</i>	19 (100%)	0	0	0	0	19
<i>oronensis</i>	0	19 (100%)	0	0	0	19
<i>ovalis</i>	0	0	15 (80%)	1	3	19
<i>tessellata</i>	0	0	0	18 (95%)	1 (5%)	19
<i>tincta</i>	1 (5%)	0	0	0	18 (95%)	19
Total	20	19	15	19	22	95

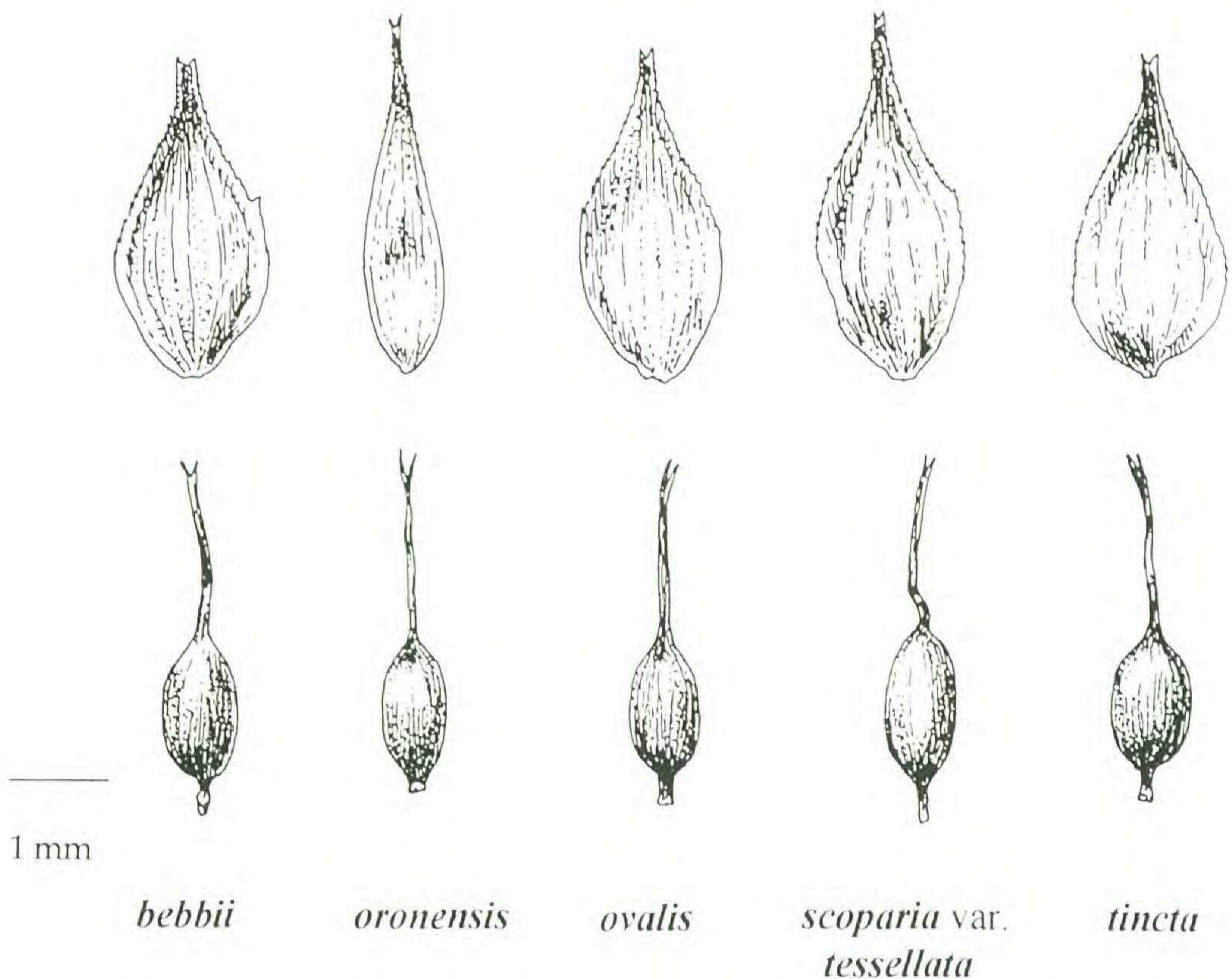


Figure 3. Perigynia and achenes of *Carex bebbii*, *C. oronensis*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria*.

for separating this species from the other four taxa included absence of a wing below the middle of the perigynium, pearly appearance of the perigynium adaxial epidermis, lack of prominent adaxial perigynium nerves, presence (in 68% of our sample) of a rust-colored blotch on the perigynium adaxial epidermis, and lack of spongy thickening on the inside wall of the perigynium at the base of the achene (Table 4). Mature perigynia are required to distinguish *C. oronensis* from *C. ovalis* or *C. scoparia* var. *tessellata*. In the upcoming *Flora of North America* treatment of *Carex*, the distance from achene summit to beak apex is 1.2–2 mm in *C. ovalis*, and greater than 2 mm in *C. scoparia* var. *tessellata* (A. A. Reznicek, pers. comm.). We did not include this variable in our study, and this might have contributed to the failure of these two taxa to separate well in Figure 2. In the field these three Maine *Ovales* are distinctive for their dark scales that almost equal the perigynium in length. Characters especially useful for distinguishing *C. oronensis* in the field are perigynium width, texture, and rusty blotch when present.

Table 3. Mean \pm SD (range) for quantitative variables that distinguish *Carex oronensis* from *C. bebbii*, *C. ovalis*, *C. scoparia* var. *tessellata*, and *C. tinctoria* [Tukey's Studentized Range (HSD) test]. Lengths and widths in mm. Means within a row followed by the same letter are not significantly different ($P = 0.05$). N = 19 for each taxon. * = distance from base to maximum width along axis. † = count variable, thus Tukey multiple comparisons of means not appropriate.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tinctoria</i>
Scale length	2.66 \pm 0.17 a (2.34–2.94)	3.48 \pm 0.22 b (3.06–3.85)	4.07 \pm 0.33 c (3.33–4.48)	3.73 \pm 0.22 d (3.32–4.12)	3.32 \pm 0.28 b (2.63–3.72)
Scale width	0.89 \pm 0.10 a (0.69–1.12)	1.24 \pm 0.09 b (1.02–1.40)	1.31 \pm 0.12 b (1.11–1.52)	1.05 \pm 0.11 c (0.87–1.26)	1.26 \pm 0.15 b (0.83–1.57)
Perigynium length	3.08 \pm 0.22 a (2.75–3.49)	3.71 \pm 0.26 b (3.25–4.12)	4.08 \pm 0.29 b (3.60–4.56)	4.39 \pm 0.31 c (3.58–4.89)	3.85 \pm 0.32 b (3.18–4.36)
Perigynium width	1.29 \pm 0.10 a (1.04–1.47)	1.10 \pm 0.11 b (0.88–1.30)	1.73 \pm 0.17 c (1.45–2.05)	1.83 \pm 0.10 c (1.57–1.96)	1.72 \pm 0.21 c (1.20–1.99)
Perigynium distance*	1.14 \pm 0.15 a (0.92–1.58)	1.32 \pm 0.19 b (0.86–1.66)	1.45 \pm 0.19 b (1.10–1.94)	1.52 \pm 0.17 b (1.28–1.92)	1.47 \pm 0.16 b (1.12–1.78)
Perigynium ab. nerves†	5.2 \pm 1.6 (1.2–7.4)	10.40 \pm 1.26 (8.40–12.60)	7.50 \pm 1.53 (3.60–9.75)	6.05 \pm 1.62 (0.80–8.80)	6.56 \pm 1.12 (3.40–8.40)

Table 3. Continued.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>
Distance to serrulation	1.13 ± 0.18 a (0.78–1.56)	1.52 ± 0.20 b (1.00–1.84)	1.69 ± 0.26 b (1.20–2.16)	1.24 ± 0.19 c (0.98–1.64)	1.62 ± 0.15 b (1.32–1.86)
Wing width	0.23 ± 0.55 a (0.15–0.35)	0.10 ± 0.22 b (0.06–0.16)	0.31 ± 0.08 a (0.23–0.58)	0.36 ± 0.07 a (0.25–0.49)	0.28 ± 0.08 a (0.12–0.44)
Tooth length	0.04 ± 0.01 a (0.03–0.09)	0.03 ± 0.01 a (0.02–0.05)	0.04 ± 0.01 a (0.03–0.06)	0.04 ± 0.01 a (0.02–0.05)	0.04 ± 0.01 a (0.03–0.08)
Achene length	1.10 ± 0.05 a (0.93–1.18)	1.46 ± 0.08 b (1.27–1.64)	1.44 ± 0.08 b (1.32–1.57)	1.37 ± 0.04 b (1.30–1.45)	1.40 ± 0.06 b (1.29–1.50)
Achene width	0.68 ± 0.05 a (0.56–0.79)	0.85 ± 0.12 a (0.62–1.26)	1.02 ± 0.12 b (0.76–1.29)	0.77 ± 0.03 a (0.72–0.83)	0.99 ± 0.15 b (0.79–1.30)
Stipe length	0.40 ± 0.05 a (0.29–0.48)	0.29 ± 0.06 b (0.10–0.35)	0.54 ± 0.09 c (0.31–0.64)	0.54 ± 0.12 c (0.18–0.64)	0.38 ± 0.08 a (0.20–0.55)

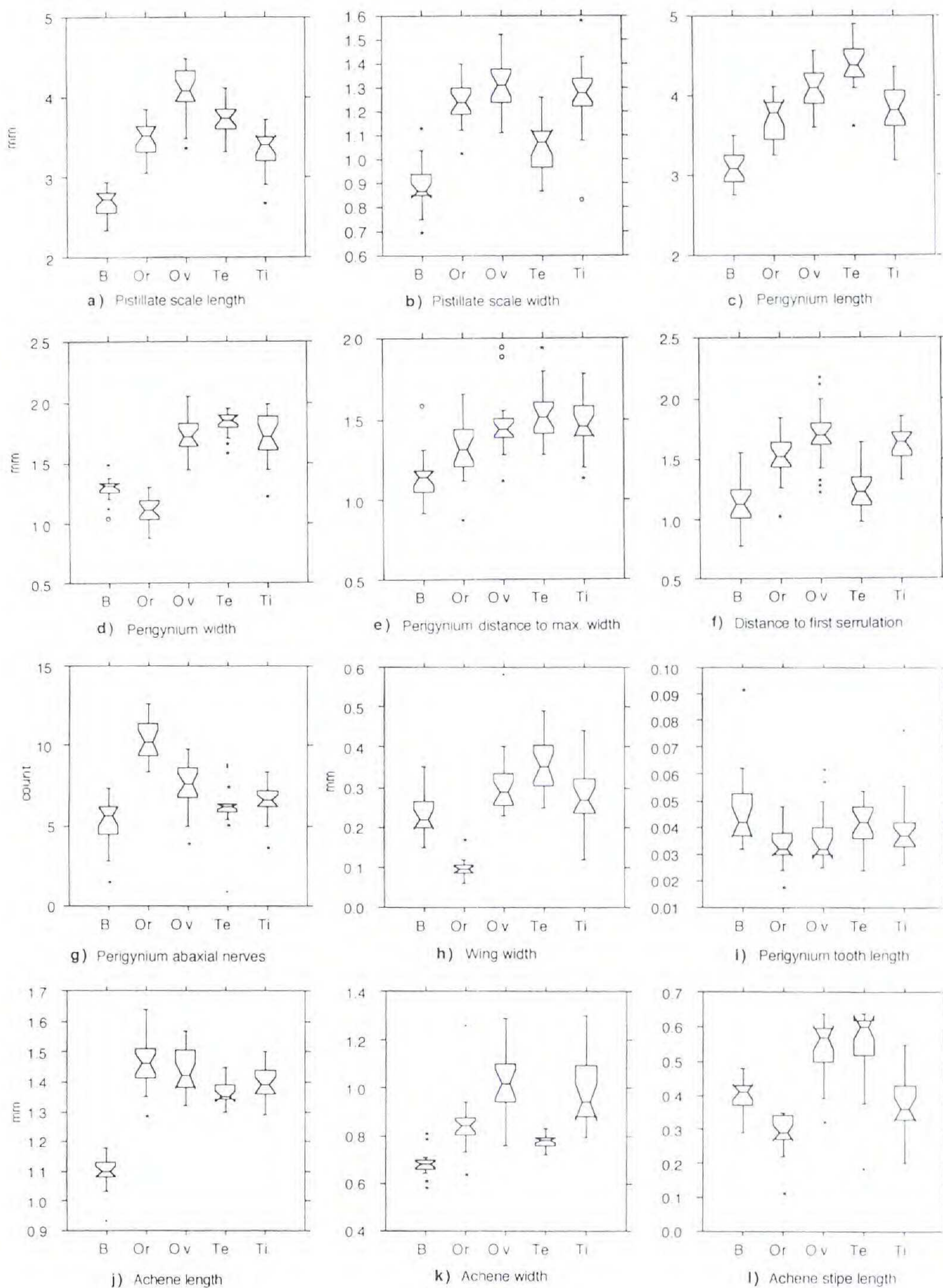


Figure 4. Notched box plots of five *Carex* species and 12 quantitative variables for reproductive structures listed in Table 1. B = *C. bebbii*, Or = *C. oronensis*, Ov = *C. ovalis*, Te = *C. scoparia* var. *tessellata*, Ti = *C. tincta*.

Table 4. Summary of morphological characters that distinguish *Carex oronensis* and four taxa that resemble it.

Character	Taxon				
	<i>bebbii</i>	<i>oronensis</i>	<i>ovalis</i>	<i>tessellata</i>	<i>tincta</i>
Mean perigynium width	1.3 mm	1.1 mm	1.7 mm	1.8 mm	1.7 mm
Pistillate scale length in relation to perigynium	Shorter	(Usually) subequal	Subequal	Shorter	Shorter
Wing below middle of perigynium	Present	Narrow or lacking	Present	Present	Present
Texture of adaxial surface of perigynium	Dull	Pearly	Dull	Dull	Dull
Adaxial nerves	Strong	Usually weak	Strong	Strong	Strong
Number of abaxial nerves	4–7	8–15	4–10	1–9	3–9
Rust-colored blotch on perigynium adaxial surface	Absent	Present in ca. 88%	Absent	Absent	Absent
Sponginess at base of achene within perigynium	Present	Absent	Present	Present	Present
Achene stipe length	Long	Short	Long	Long	Intermediate

Carex tinctoria was often 20–40 cm taller than *C. oronensis* and *C. ovalis*, with a thicker stem, fewer fertile culms per individual, wider spikes, fewer flowers per spike, perigynium beak visible above the shorter scales, and the perigynium adaxial surface usually flattened. Also, its perigynia were almost completely dispersed by late July, while *C. oronensis* often retained a few perigynia in the spike through the succeeding winter. Perigynia in *C. tinctoria* were usually sessile, while those of *C. oronensis* and *C. ovalis* were usually short-stalked.

Carex bebbii differed from the other species in this study in its more tightly aggregated inflorescence, compact spikes, short and narrow pistillate scales, shorter distance from the base to the widest part of perigynium, and tendency to occur in wetter habitats. This species was sympatric with *C. oronensis* along a gravelly railroad landing, a site that is uncharacteristic for *C. bebbii* in Maine; this suggests that the amplitude for habitat preference in *C. bebbii* might be greater than often assumed.

Other taxa in sect. *Ovales* that occur within the range of *Carex oronensis*, and with which it might be confused, include *C. crawfordii* Fernald and *C. tribuloides* Wahlenb. Both have as narrow a perigynium, but both differ from *C. oronensis* in leaf width, scale color, scale length and width, perigynium shape and texture, achene dimensions, and, in *C. crawfordii*, style configuration (contorted versus straight in *C. oronensis*). *Carex foenea* Willd. (syn. *C. aenea* Fernald) occasionally has a long bract subtending the inflorescence, its scales equal or exceed perigynia in length, and the perigynia are larger, darker, and have more prominent nerves than those of *C. oronensis*, *C. ovalis*, or *C. scoparia* var. *tessellata*. The achenes of *C. foenea* are dark brown when ripe, while those of the other three taxa are light to medium brown.

Geographical distribution, population size, and habitat characteristics. During field surveys conducted between 1987–98, we and others located 58 populations and 2862 individuals of *Carex oronensis*; this expanded the known range by more than 100 km in several directions (Figure 1). All populations occurred in the Penobscot River drainage except for two small populations in the adjacent Kennebec drainage (most sites listed in Dibble 1991).

Plant size and population density (counted number of individuals per estimated area at each site) were greatest in mesic mead-

ows in full sun. The largest populations of *Carex oronensis* were within 2 km of the Penobscot River in old hay fields that were mowed every few years. Distribution of population size was strongly skewed toward small populations. Eighty percent of extant populations had fewer than 20 individuals, 22% had only one or two individuals, and only two populations contained more than 300 individuals.

Carex oronensis occurs in open habitats on various soil types from sand to fine silt loam—the “argillaceous meadows” of Fernald’s herbarium labels from 1916. Habitats include hay fields, old fields, sandy roadsides, powerlines, borders of cultivated fields, edges of commercial and residential establishments, rivershore, gravel pits, swales, woods roads, an alluvial oak forest, and a former sawmill site. Soil moisture ranges from seasonally inundated to dry. Elevation is not known to exceed 360 m and slope ranges from none to 30%. Occurrences are often surrounded by apparently suitable habitat not occupied by *C. oronensis*.

Associated vegetation. For 49 of the 58 *Carex oronensis* populations, we found a total of 10 other species in sect. *Ovales*, with varying numbers of sites at which they were found [*C. bebbii* 1, *C. crawfordii* 8, *C. foenea* (formerly *C. aenea*) 1, *C. merritt-fernaldii* Mack. 2, *C. normalis* Mack. 3, *C. projecta* Mack. 9, *C. scoparia* var. *scoparia* 20, *C. tenera* 13, *C. tinctoria* 13, and *C. tribuloides* 4]. *Carex scoparia*, *C. tenera*, and *C. tinctoria* were the most common sympatric species and these are common throughout much of the range of *C. oronensis*, especially on roadsides. We did not observe *C. scoparia* var. *tessellata* or *C. ovalis* growing with *C. oronensis*, and we have not often found *C. ovalis* in Maine. *Carex* in sections other than sect. *Ovales* that were common in *C. oronensis* sites included *C. gracillima* Schwein. and *C. pallescens* L. Other associated vegetation includes many non-native (according to Campbell et al. 1995; Haines and Vining 1998), early successional herbs such as *Rumex acetosella* L., *Leucanthemum vulgare* Lam., *Ranunculus acris* L., *Anaphalis margaritacea* (L.) Benth. & Hook. f., *Achillea millefolium* L., *Phleum pratense* L., *Trifolium* spp., *Vicia cracca* L., and *Hieracium* spp. Native associates include *Juncus* spp., *Luzula* spp., *Panicum* spp., *Solidago* spp., *Rubus idaeus* L., *Apocynum androsaemifolium* L., *Salix* spp., and *Spiraea alba* Du Roi var. *latifolia* (Aiton) Dippel.

Table 5. Percent fruit set, seed germination, pollen stainability, and pollen germination in *Carex oronensis*. N = number of individuals.

Character	N	Sample per Individual	Percent		
			Mean	SD	Range
Fruit set	5	28 flowers	90.6	5.4	80.3–97.2
Seed germination	5	97, 53, 42, 83, 70	27.7	36.5	8.2–92.8
Pollen stainability	5	>200 grains	88.5	5.4	79.5–94.2
Pollen germination	4	>200 grains	70.0	17.4	51.6–90.0

Reproductive ecology and results of compatibility experiments. *Carex oronensis* is usually protogynous, but anthers dehisce within a few days of stigma receptivity and stigmas and anthers are often presented simultaneously. Anthesis occurs from late May to mid-June, overlapping that of many sympatric *Carex* species but often preceding *C. tinctoria* by one to two weeks. Anthesis and fruit maturation can occur at the same time within an individual, but later flowers are smaller and less likely to yield fruits. Mean fruit set, pollen germination, and pollen stainability equalled or exceeded 70%, while seed germination averaged 27.7% (Table 5). Controlled self-pollinations and intraspecific crosses of *C. oronensis* yielded at least some viable seeds per inflorescence. Open-pollinated seed of *C. oronensis* planted in the common garden produced offspring indistinguishable from *C. oronensis*. Casual observations suggest dispersal by wind, water, and gravity from late June through October and in early spring.

We counted the haploid chromosome number for *Carex oronensis* as $n = 34$ in multiple cells in one individual (voucher for population *Dibble 72*, see Appendix; voucher for this same individual, *Dibble 10020*, 1 Jul 2001, MAINE).

DISCUSSION

Conservation of *Carex oronensis* would be difficult or impossible if it was not morphologically distinct. Our results clarify and reinforce Fernald's (1902, 1950) perception of this as a discrete entity. One character not mentioned by Fernald that is useful when present is the rust-colored blotch on the adaxial surface of the perigynium. Few eastern North American *Ovales* feature this, even occasionally. Some western North American *Ovales* bear a

rust-colored blotch, but our sample size was too small to determine whether this is consistent throughout the range of such taxa. Of the specimens with a rust-colored blotch that we examined, only *C. oronensis* consistently lacked basal sponginess about the achene.

We have seen a few populations of *Carex oronensis* disappear since we first found them, though the seed bank might hold this species. Small populations are not unusual in many *Carex* species (Richards 1986), and Reznicek (1986) usually found Mexican and Central American *Carex* in sect. *Hymenochlaenae* in predominantly small, widely dispersed populations.

Nineteenth century loggers may have influenced the distribution of *Carex oronensis* through the practice of supplying hay (containing seed of *C. oronensis*) to logging camps within the same watershed where trees were harvested, with little commercial exchange between watersheds. The two *C. oronensis* populations that occurred outside the Penobscot River drainage were along a former supply route to the West Branch of the Penobscot River. The presence of these populations in the Kennebec River drainage could be explained by hay shipments from the Bangor area (in the lower Penobscot River drainage) along Moosehead Lake (in the upper Kennebec River drainage) to Pittston Farm (in the upper West Branch of the Penobscot River drainage), which is a former supply center for loggers on the West Branch and a current site for *C. oronensis*. This method was suggested for the eastward expansion of *C. praegracilis* W. Boott along railways (Reznicek and Catling 1987). Similarly, *C. crawfordii* was introduced to Great Britain from North America with crop seed (Jermy et al. 1982). The proximity of *C. oronensis* to the Penobscot River or one of its tributaries may also reflect some habitat conditions that we have not yet recognized or quantified.

The chromosome count for *Carex oronensis* was $n = 34$ in our study, and $n = 37$ in Rothrock and Reznicek (1996a). It is not known whether this variation is due to aneuploidy, which is prevalent in *Carex* and thought to influence speciation in this genus (Grant 1981). There is an opportunity for recombination through agmatoploidy, in which chromosome fragments retain viability because of the diffuse centromere (Davies 1956), and such fragments of chromosomes are capable of surviving from one generation to the next (Rothrock and Reznicek 1996a). Variation in chromosome number within species may be considerable in sect.

Ovales (Whitkus 1991). Agmatoploidy presumably may decrease or increase chromosome number (Reznicek 1990). Chromosome number may vary among cells of one individual or more often at intra- and interpopulation levels in some species in sect. *Ovales*. However chromosome number in *Carex* is generally considered stable, so such variation could be due to misidentification of taxa in at least some cases (Whitkus 1991).

Status and possible origin of *Carex oronensis*. *Carex oronensis* deserves species status because it is morphologically distinct, has a well-defined geographic range, bears fertile seed and pollen, and has the ability to breed true. We found no intergradation between this species and any other.

Carex oronensis, with $n = \text{ca. } 34, 37$, could have resulted from chromosome breakage in *C. ovalis* ($n = 32, 33$, and 34 ; all counts from Europe), *C. tinctoria* ($n = 36 + \text{IV}$ from one plant only; Rothrock and Reznicek 1996a), or *C. scoparia* var. *tessellata* ($n = 33$ from several sites; P. E. Rothrock, pers. comm.).

While polyploidy and hybridization are known in *Carex* (Cayouette and Catling 1992; Grant 1981) and sect. *Ovales* (Rothrock and Reznicek 1996b; Rothrock et al. 1997), our data do not support the suggestion that *C. oronensis* is of hybrid origin. Fernald (1950) claimed hybridization among six species, not including *C. oronensis*, within eastern North American members of sect. *Ovales*. *Carex* hybrids are often sterile (Eaton 1957; Whitkus 1988), but sterile or poorly developed individuals that are not hybrids are also fairly frequent in *Carex* whether or not the species is self-compatible (A. A. Reznicek, pers. comm.). Such depauperate individuals could result from disease, herbivory, or insufficient pollination due to adverse weather during anthesis. We found three sterile individuals that are morphologically more or less intermediate (in features other than filled achenes, which were lacking) between *C. oronensis* and *C. tinctoria* and one sterile intermediate between *C. oronensis* and *C. scoparia*; all were from the largest known population, which is in Orono. We could not assign parentage to numerous sterile individuals from a site in Carroll where *C. oronensis* was present. Otherwise, we encountered few apparent hybrids for which *C. oronensis* is a possible parent.

Firm evidence regarding the nonhybrid origin of *Carex oronensis* is lacking, but the plausibility of various hypotheses can

be considered. If *C. oronensis* is a relict whose formerly widespread distribution has been reduced by climate change, as with some serpentine-adapted *Carex* endemics (Waterway 1990), then we would expect the distribution to include widely disjunct populations. Paleoendemism seems unlikely for *C. oronensis* because it is confined to an area that was recently covered by glacial ice and its apparently suitable habitat is widely distributed.

We speculate that limited distribution in a recently glaciated region, and relatively narrow intraspecific variation in morphology, suggest that *Carex oronensis* is a young taxon. A single evolutionary event could have led to divergence from an unidentified parent since the Laurentian ice shield receded about 13,000 years ago. A scenario suggested to us informally by A. A. Reznicek (pers. comm.) is plausible: during the pleistocene *C. oronensis* might have been restricted to sandy river terraces, and these gradually became forested. The agricultural activities of early native Americans and later of European settlers led to an expansion of early successional habitat near rivers. In the 18th and 19th centuries, river impoundments might have altered the sandy river bar and terrace habitat; this could have led to association of *C. oronensis* more with human disturbance than with river dynamics. Recently, dispersal of *C. oronensis* could be through transport of hay. Lack of dispersal beyond two river drainages in Maine could be due to some biological feature that limits colonization by *C. oronensis*, such as low germination rate or seedling survival rate under natural conditions, or a short life span that prevents dissemination of many propagules over a period of years. We know of no data to support these suggestions.

Ovales of the southeastern United States have been studied by Rothrock and Reznicek (1996b). Derivation from a species of that region, during or following the maximum extent of the Wisconsin glacier, seems unlikely because *Carex oronensis* is morphologically dissimilar to such taxa. Derivation from *Ovales* of western North America, including species from potential refugia in the Rocky Mountains and near the Pacific Coast, appears improbable because *C. oronensis* does not resemble them, either. It does share morphological features with two Eurasian *Ovales*: *C. ovalis* and *C. macloviana* (which grows in North America as well, and differs from *C. oronensis* especially in its metallic appearance of the perigynia, presence of spongy tissue at base of achene, and fewer abaxial nerves on the perigynium). Both of these Eurasian taxa

have dark scales that equal or exceed the perigynium in length; however, both lack the narrow perigynium of *C. oronensis*. The perigynium of *C. macloviana* is distinctly longer and wider than that of *C. oronensis*.

Carex oronensis could have arisen from *C. ovalis*, a weedy species of Europe (Kukkonen and Toivonen 1988). As with some other plants adventive to North America (Faden 1989; Reznicek and Catling 1987), arrival time, place, and means are unknown. Fernald (1902) thought that *C. ovalis* was “doubtless introduced” in New Jersey but was “perhaps indigenous northward,” or “naturalized from Europe” (Fernald 1950). The earliest collection in North America that we have seen is that of W. Boott from Long Island, Boston Harbor, Massachusetts in 1871 (NY). *Carex ovalis* was divided into at least three subspecies, but these were rarely applied to North American collections and are no longer recognized (Chater 1980; Jermy et al. 1982). Some Eurasian specimens show marked variation and differ morphologically from North American *C. ovalis* in habit, plant height, number of spikes per culm, and in other features of the inflorescence, although perigynia approximate those of North American *C. ovalis*.

Definitive identification of a closest relative or parent taxon for *Carex oronensis* may require a molecular study including much of sect. *Ovales*. Morphology, chromosome numbers, reproductive biology, and habitat preferences will enhance such a study but cannot, in themselves, be used to assign relatedness for this species.

Implications for conservation and management of *Carex oronensis*. Because *Carex oronensis* is a distinct taxon (see description), with a well-defined geographical distribution and ephemeral habitat in the absence of human intervention, management recommendations are straightforward. Given the intensity of habitat disturbance with which this species is associated, populations could be short-lived and difficult to conserve unless mowed or perhaps burned on an annual or biennial schedule. Ideally, such treatment would be conducted after seeds have dispersed, thus no sooner than late July. Further field survey might reveal that mowing obscures populations and maintains them in a vegetative state, and more populations are likely to be found. Field checks for most of the 58 known sites have not been conducted since they were first observed in the late 1980s, and no

demographic studies have been undertaken. There are no data regarding dispersal capability, fecundity, survivorship, longevity of individuals, and persistence of populations. This globally rare taxon is currently without any regulatory protection on either the federal or state level. Only four of the 58 known populations are on public lands and there, habitat is kept open by mowing or by timber harvest activities in the vicinity. Additional research regarding phylogeny and population viability could provide a better picture of relatedness and assure that, where protection can be undertaken, this species does not reach irrecoverably low population size.

DESCRIPTION

Carex oronensis Fernald, Proc. Am. Acad. 37: 471. 1902.

LECTOTYPE designated here: UNITED STATES. Maine: Orono, dry fields, etc. [*sic*], 30 Jun 1891, *Fernald s.n.* GH! (Originally identified by Fernald as "*Carex scoparia* Schk. forma").

Plants loosely caespitose; roots black, fibrous. Fertile culms 30–100 cm, exceeding leaves in height, scabrous below the inflorescence. Cauline leaves 3–4 per fertile culm, 2–4 mm wide. Inflorescences 1.5–3.4 × 0.6–1.5 cm; spikes aggregate, usually (3) 5–6 (10), gynecandrous, 5–10 × 3–7 mm, each spike with 14–36 pistillate and 6–12 staminate flowers. Pistillate scales acute to acuminate or rounded, nearly equal to perigynia in length, 3.1–3.9 × 0.9–1.6 mm, chestnut-brown, glossy, with pale midvein and hyaline margins. Perigynia lanceolate or oblanceolate, light green to straw-colored, usually bearing a rust-colored blotch on adaxial surface, 2.9–4.3 long × 0.9–1.4 mm wide, wingless below the middle, wings slightly toothed toward apex, with adaxial epidermis pearly in appearance, usually lacking prominent nerves or with 5–7 obscure nerves, abaxial nerves 7–15; beak tip to top of achene 1.5–2.4 mm; beak tip hyaline; ventral suture usually with hyaline margin; spongy tissue at base of achene lacking. Achenes light brown, body 1.3–1.6 × 0.7–1.4 mm; achene stipe 0.2–0.4 mm long; style straight; stigmas 2, red-brown. $n = 34, 37$.

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APPENDIX

SPECIMENS USED IN MORPHOLOGICAL STUDY

Carex bebbii Olney

UNITED STATES. Maine: Aroostook Co., Houlton, Carey's Mills, near Meduxnekeag River in low wet area, 30 Jun 1988, *Dibble* 945 (MAINE); Linneus, Rt. 2A, dooryard of old farmstead, 7 Jul 1988, *Dibble* 1324 (MAINE); Penobscot Co., Bangor, Air National Guard Base W of city, roadsides, 19 Jul 1991, *Dibble* 3693 (MAINE); Holden, Hog Hill, logging road upper NE slope, 17 Jul 1992, *Dibble* 4137-4138 (MAINE); Masardis, in gravel at RR track, site of old RR station, 6 Jul 1988, *Dibble* 1280 (MAINE); Orono, swale, 27 Jun 1891, *Fernald* s.n. (NHA); Orono, Rt. 2, gravel near RR track, 5 Jul 1991, *Dibble* 3664 (MAINE); Orono, Rt. 2, gravel near RR track, 10 Jul 1992, *Dibble* 4139-4142 (MAINE); Prentiss, Rt. 169, roadside bank, 1 Jul 1988, *Dibble* 970 (MAINE); Piscataquis Co., Dover, low thicket, 15 Jul 1895, *Fernald* 284 (L. A. Standley). Massachusetts: Berkshire Co., Monterey, unshaded fen along Konkapot River, 4 Jul 1991, *Rothrock* 2342 (MAINE); Essex Co., W. Manchester, railroad side, 30 Jun 1911, *Hubbard* 61a (MAINE). Michigan: Kalamazoo Co., Kalamazoo, brushy marsh, 23 Jun 1992, *Rothrock* 2518 (MAINE); Vicksburg, black muck soil in willow swamp/dogwood thicket, 25 Jun 1982, *Rothrock* 1605 (MAINE). Pennsylvania: Centre Co., State College, calcareous swamp with *Typha* and *Carex stricta*, 1 Jul 1975, *Rothrock* 615 (MAINE).

Carex oronensis Fernald

UNITED STATES. Maine: Aroostook Co., Haynesville, roadside, 7 Jul 1988, *Dibble* 1312 (MAINE); Molunkus, dooryard of former homestead, 13

Jul 1987, *Dibble 143* (MAINE); Sherman, edge of potato field, 1 Jul 1988, *Dibble 1176* (MAINE); Penobscot Co., Bangor, compost heap at Mt. Hope cemetery, 22 Jun 1988, *Dibble 1073* (MAINE); Carroll Plantation, North Rd., King Farm, old field, 5 Jul 1988, *Dibble 1246* (MAINE); Medway, Rt. 11 along E. shore, East Branch, Penobscot River, vacant lot in residential area, 13 Jul 1987, *Dibble 146* (MAINE); Old Town, alluvial woods on banks of Stillwater River in old gravel pit, dry sandy soil, 12 Jul 1987, *Dibble 121* (MAINE); Orono, type locality, argillaceous meadows, 27 Jun 1916, *Fernald 152*, PLANTAE EXSICATTAE GRAYANAE (MICH); Orono, roadside SW jct. Stillwater Ave. and Forest Ave., 22 Jun 1988, *Dibble 1062* (MAINE); Orono, Gardner Rd., old field, 3 Jul 1987, *Dibble 72* (MAINE); Passadumkeag, E shore Penobscot River, rocky rivershore, 30 Jun 1988, *Dibble 1163* (MAINE); Prentiss, old fields, roadside, jct. Rt. 171 and shortcut W to Rt. 170, 1 Jul 1988, *Dibble 1173* (MAINE); Winn, Rt. 2, roadside, dry soil, 13 Jul 1987, *Dibble 139* (MAINE); T3 R7 WELS, Hunt Farm, opening at roadside, E shore, East Branch, Penobscot River, 1 Jul 1988, *Dibble 1181* (MAINE); T 4 Indian Purchase, woods road E of North Twin Lake, 28 Jun 1988, *Dibble 1157* (MAINE); Piscataquis Co., Monson, Rt. 6/15, hayfield, 28 Jun 1989, *Dibble 2200* (MAINE); T6 R9 WELS, Trout Brook Farm, Baxter State Park, open meadow to N of ranger cabin, 6 Jul 1988, *Dibble 1257* (MAINE); T7 R11 WELS, Pinkham Rd. NE of Carpenter Mt., roadside, 23 Jun 1989, *Dibble 2151* (MAINE); Somerset Co., T2 R4 NBKP, Pittston Academy Grant, Pittston Farm, old fields near Penobscot River to NE of farmstead, 28 Jun 1989, *Dibble 2208* (MAINE).

Carex ovalis Gooden.

ARMENIA (Transcaucasia). distr. Nor. Bajazet, 3 Aug 1928, collector unknown (NY).

CANADA. New Brunswick: Carleton Co., Woodstock, roadside ditch along Trans Canada Hwy., 25 Jul 1988, *Dibble 1600* (MAINE); York Co., Fredericton, The Hermitage, terrace above St. John River, 25 Jul 1988, *Dibble 1615*, *Hinds & Rooney* (MAINE). Newfoundland: Cape Ray, woods near Table Mt., 7 Jul 1912, *Curtis 21-18-20-221* (MAINE).

FRANCE. Moniturts Basin, Alps, Ch. d'Allerzette, 16 Jul 192?, collector unknown (MICH).

GERMANY. Mecklenburg, 14 Aug 1987, *Siering s.n.* (MICH).

NEW ZEALAND. Thomas River, Canterbury, Jan 1 1973, *Thompson 370* (MICH).

NORWAY. Ved Vrietiania, 1883, *Duhl s.n.* (BH).

SPAIN. LaRioja: Logrono, Iberica San Millan de la Cogolla, prado humados 1800 m, 29 Jul 1987, *Luceno & Vargas 2446* (MICH); Lusitania: Lameiro da Quinta do Rio Frio, Arredores da Guarda, 12 Jun 1949, *Fernandes & Lausac s.n.* (BH).

SWEDEN. "Suburb of Stockholm", 3 Jul 1949, *Ohlsen s.n.* (NY).

UNITED STATES. Maine: Aroostook Co., Orient, Rt. 1 at Weston town line, 7 Jul 1988, *Dibble 1335* (MAINE); Penobscot Co., Carroll Plantation, North Rd., King Farm, swale in old field, 5 Jul 1988, *Dibble 1247* (MAINE); Orono, low pasture, 22 Jul 1916, *Fernald & Long 1296* (NHA); Oxford Co., Canton, dry rocky pasture, 21 Jun 1908, *Parlin s.n.* (MAINE). Massachusetts:

Norfolk Co., Dedham, dry field, 4 Jul 1907, *Bartlett 792* (MICH). New Hampshire: Rockingham Co., Hampton Falls, Newfound Hill, 17 Jun 1900, *Easton s.n.* (MICH). North Carolina: Mitchell Co., Roan Mt., edge of trail in fir wood on summit, ca. 6200 ft., 11 Jul 1959, *Hermann 15209* (MICH).

USSR. Leningrad region, 25 Jul 1964, *Chater s.n.* (MICH).

Carex scoparia Schkuhr ex Willd. var. *tessellata* Fernald & Wiegand

UNITED STATES. Maine: Hancock Co., T 9 SD, bottom of moist sandy borrow pit, 11 Jul 1995, *Dibble 4816 & Rothrock* (MAINE); Penobscot Co., Prentiss, 1 Jul 1988, *Dibble 1199*, (MAINE); Washington Co., Addison, sandy roadside, 22 Jul 1995, *Dibble 4818* (MAINE); Columbia Falls, sandy roadside, 22 Jul 1995, *Dibble 4815* (MAINE); Jonesport, in Sphagnum moss next to freshwater pond NE of Sandy River Beach, 7 Jul 1993, *Lewis s.n.* (Univ. Maine at Machias Herbarium); Jonesport, Sandy River Beach, 17 Jul 1992, *Reznicek 9154* (MAINE); Machias, Cross Rd., swale along roadside, with *C. scoparia*, 23 Jul 1988, *Dibble 1592* (MAINE); Pembroke, dry low ground, 8 Jul 1909, *Fernald 1464* (NY); Roque Bluffs, 23 Jul 1988, *Dibble 1588-1591, 1593, 1596, 1597, 2400* (MAINE); Unionville, sandy roadside at edge of blueberry field, 11 Jul 1995, *Dibble 4817, 4819 & Rothrock* (MAINE). New York: Long Island, Montauk, sandy shores at Great Pond or Point, 4 Jul 1927, *Latham 4146* (NY).

Carex tinctoria Fernald

CANADA. Alberta: Fort Saskatchewan, in "grassy slough", 11 Sep 1956, *Turner 9430* (MICH). New Brunswick: North Co., confluence Miramichi and Renous River, dry bank, 22 Jun 1978, *Hinds & Breen 481* (UNB); York Co., Nortondale, West Branch, Nackawic Str., dry roadside at swampy woods at jct. Rt. 585/Rt. 595, 25 Jun 1982, *Hinds 6005* (UNB). Ontario: Thunder Bay, lakeshore at Roundtable Lake, 18 Jul 1951, *Garton 1440* (NY).

UNITED STATES. Maine: Aroostook Co., Fort Fairfield, dry soil, 12 Jul 1893, *Fernald 165* (L. A. Standley); Fort Fairfield, roadside, 1 Jul 1940, *Chamberlain 1702* (MAINE); Haynesville Ferry Bridge, roadside, 7 Jul 1988, *Dibble 1311* (MAINE); Hersey, roadside bank, Rt. 11, 6 Jul 1988, *Dibble 1255* (MAINE); Mapleton, dry field, 12 Jun 1941, *Chamberlain 2618* (MAINE); Presque Isle, roadside swamp, Washburn Rd., 1 Jul 1939, *Chamberlain 1139* (MAINE); Penobscot Co., Carroll Plantation, North Rd., King Farm, swale in old field, 5 Jul 1988, *Dibble 1234* (MAINE); Charleston, wet ditch by roadside, 4 Jul 1905, *Knight s.n.* (MICH); Medway, dry soil, Rt. 11, vacant lot, 13 Jul 1988, *Dibble 147* (MAINE); Orono, dry soil, 12 Jul 1890, *Fernald 1231* (MAINE); Piscataquis Co., Monson, Rt. 6 hayfield, old field, 28 Jun 1989, *Dibble 2201* (MAINE); Somerset Co., T2 R4 NBKP, Pittston Academy Grant, Pittston Farm, old fields near Penobscot River to NE of farmstead, 28 Jun 1989, *Dibble 2207* (MAINE). Massachusetts: Hampshire Co., Middlefield, hillside meadow, 26 Jun 1913, *Fernald & Long 8982* (NY.). New Hampshire: Coos Co., Jefferson, meadow, 3 Jul 1950, *Pease s.n.* (NHA). Vermont: Caledonia Co., St. Johnsbury, meadow, 2 Jun 1901, *Hazen 206* (VT).